

# Current Biology

## A New Burgess Shale Polychaete and the Origin of the Annelid Head Revisited

### Highlights

- An abundant Cambrian polychaete preserves exceptional morphological details
- The new species possesses a median antenna and large palps on the prostomium
- Neuropodial chaetae are present on the mouth-bearing peristomium
- A chaetigerous origin for the peristomial portion of the annelid head is proposed

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### In Brief

Fossilized annelids are very rare. Nanglu and Caron describe an abundant and exceptionally well-preserved new species from the 508-million-year-old Burgess Shale. The new species sheds light on the origin of the annelid head and suggests a segmental origin for the mouth-bearing segment.



# A New Burgess Shale Polychaete and the Origin of the Annelid Head Revisited

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## SUMMARY

Annelida is one of the most speciose (~17,000 species) and ecologically successful phyla. Key to this success is their flexible body plan with metameric trunk segments and bipartite heads consisting of a prostomium bearing sensory structures and a peristomium containing the mouth. The flexibility of this body plan has traditionally proven problematic for reconstructing the evolutionary relationships within the Annelida. Although recent phylogenies have focused on resolving the interrelationships of the crown group [1–3], many questions remain regarding the early evolution of the annelid body plan itself, including the origin of the head [4]. Here we describe an abundant and exceptionally well-preserved polychaete with traces of putative neural and vascular tissues for the first time in a fossilized annelid. Up to three centimeters in length, *Kootenayscolex barbarensis* gen. et sp. nov. is described based on more than 500 specimens from Marble Canyon [5] and several specimens from the original Burgess Shale site (both in British Columbia, Canada). *K. barbarensis* possesses biramous parapodia along the trunk, bearing similar elongate and thin notochaetae and neurochaetae. A pair of large palps and one median antenna project from the anteriormost dorsal margin of the prostomium. The mouth-bearing peristomium bears neuropodial chaetae, a condition that is also inferred in *Canadia* and *Burgessochaeta* from the Burgess Shale, suggesting a chaetigerous origin for the peristomial portion of the head and a secondary loss of peristomial parapodia and chaetae in modern polychaetes.

## RESULTS AND DISCUSSION

### Systematic Paleontology

#### Phylum

Annelida Lamarck, 1809.

#### Genus

*Kootenayscolex barbarensis* gen. et sp. nov.

### Etymology

*Kootenay* for Kootenay National Park in British Columbia, Canada, where the Marble Canyon fossil locality is located, and *scolex*, the Greek word for “worm”; *barbarensis* from Barbara Polk Milstein, who is a volunteer at the Royal Ontario Museum and a long-time supporter of Burgess Shale research.

### Holotype

ROMIP64388 (Figures 1A and S2B).

### Referred Material

Paratypes: ROMIP62972, ROMIP63099.1, and ROMIP64389–64398. In addition, ~500 further specimens at the Royal Ontario Museum. See STAR Methods for locality information.

### Preservation

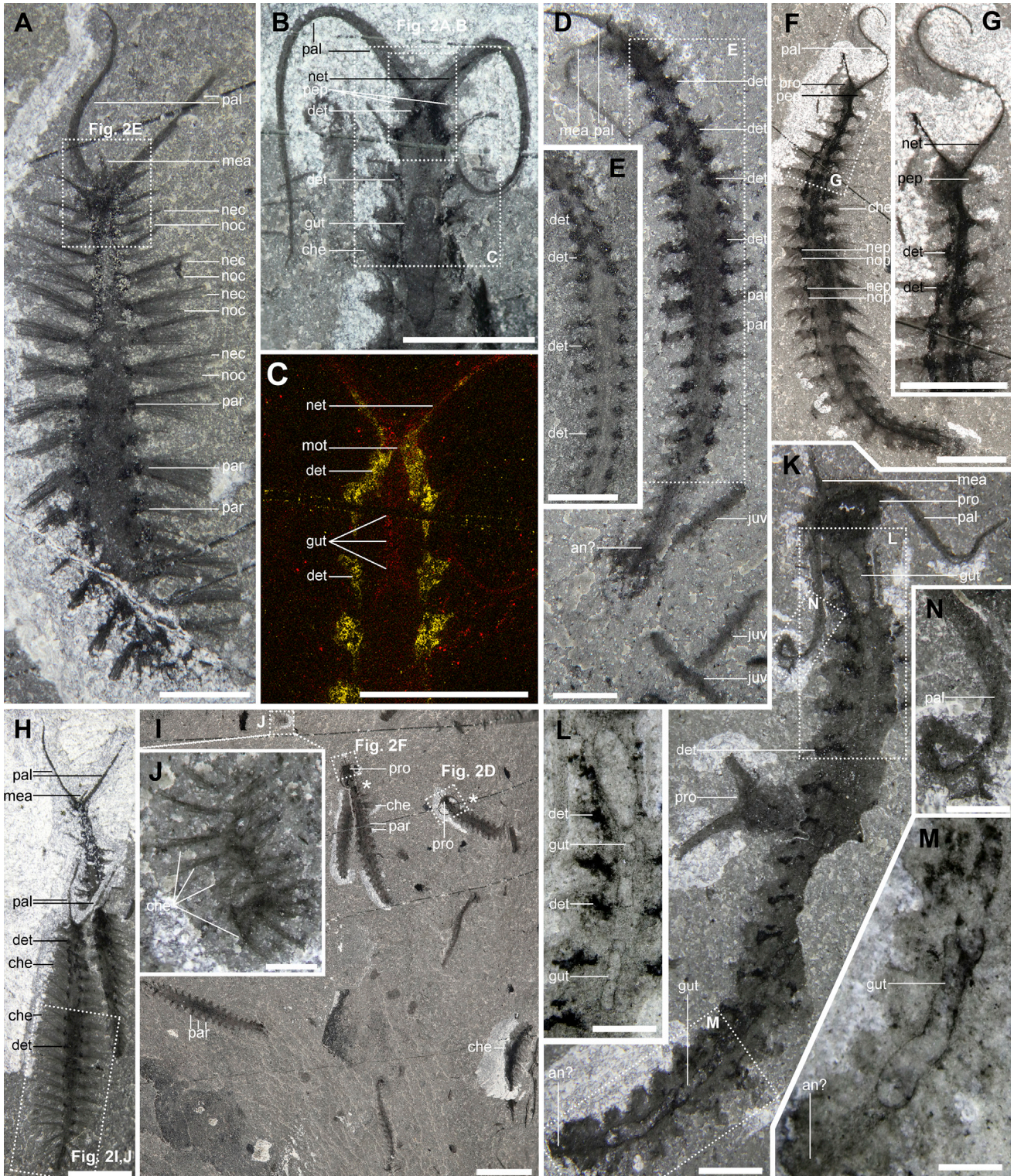
Specimens display a wide range of burial angles (Figure 1) consistent with being engulfed in fast-moving bottom mudflow deposits [6]. The chaetae are rarely preserved, possibly as a result of decay, angle of burial, and/or the composition and thinness of the individual chaetae. Dark patches occur within the base of the palps and parapodia (Figures 1B, 1C, 2A–2H, and S3C), often coalescing between adjacent parapodia and between the frontalmost parapodia and the head. In the palps, such areas may correspond to coelomic cavities (see Diagnosis), whereas they seem topographically concordant with muscle tissues and associated coelomic cavities within the parapodia [7]. These structures are phosphatized (Figures 1C and S1), which could support a musculature origin [8], although muscle tissues themselves are not preserved.

### Diagnosis

*K. barbarensis* ranges from 1 mm (Figures 1D, 1I, and 1J) to ~30 mm and possesses up to 25 chaetigers (Figure 1F). The general shape of the body is elongate and is widest at approximately the halfway point (Figures 1D, 1F, and 1H).

The anteriormost unit, representing the prostomium, is roughly trapezoidal in dorsoventral aspect and widest at the anterior end (e.g., Figures 1B, 1K, and 2A–2C). A pair of long and flexible appendages extends from the anterior dorsal edge of the prostomium (e.g., Figures 1A–1D, 1F–1H, 1K, 2A–2H, S1A, S2A–S2F, and S3A–S3F), with a more dorsally located shorter appendage between them (e.g., Figures 1A, 1K, and 2C–2E). These are interpreted as paired palps and a median antenna, respectively. The palps can reach one-third of body length (e.g., Figure 1H), possess a thick base, and taper distally to a fine point (Figures 1B–1D, 1F–1H, and 1K). When twisted, the palps appear to become slightly flattened distally (Figure 1N). A thin reflective band rich in carbon and partially phosphatized, roughly one-third





**Figure 1. General Morphology of *Kootenayscolex barbarensis* from the Burgess Shale, Marble Canyon Locality**

All images are oriented with anterior directed to the top of the page. All images were taken using cross-polarized light except (C). Acronyms: an?, anus?; che, chaetae; det, degraded tissue; gin, gut infill; gut, gut; juv, juvenile; mot, mouth; nec, neurochaetae; nep, neuropodia; net, neural tissue; noc, notochaetae; nop, notopodia; mea, median antenna; pal, palps; par, parapodia; pco, prostomial coelom; pep, peristomial parapodia; pec, peristomial chaetae; pro, prostomium. Scale bars, 1 mm. See also [Figures S1–S3](#).

(A) Holotype (ROMIP64388): nearly complete specimen (posterior missing) showing well-preserved palps, median antenna, and chaetae.

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the diameter of the palps, runs from their distal tips to the anterior of the prostomium (e.g., [Figures 1B, 1C, 2A–2C, S1D, S1G, and S2A](#)). An even darker, thinner carbon-rich structure traces the same pathway within this channel ([Figures 1C, 2A, 2C, and S1D–S1F](#)), consistent with the neural architecture of many extant polychaetes, with neural pathways converging on a dense central neuropil region in the prostomium [9–12]. The larger, lightly shaded pathway within the palps is consistent with a coelomic cavity [8] ([Figure 3](#)).

The median antenna is roughly half the thickness of the base of a palp and appears to be more rigid than the palps, further supporting its identification as an antenna [13]. A dark internal structure similar to those found in the palps seems to have a common origin within the prostomium ([Figure 2H](#)). Posteriorly, a pair of structures sometimes preserved laterally at the base of the palps ([Figures 2A–2G](#)) or directed more anteriorly, and with radiating chaetae projecting anteriorly or laterally, are interpreted as peristomial parapodia bearing chaetae. Only a single set of chaetal bundles could be observed along the peristomial parapodia, suggesting a uniramous condition. The preserved chaetal bundles are hypothesized to represent neurochaeta. The mouth is between those parapodia, as suggested by the anteriormost portion of the gut ([Figures 1B, 1C, 2A–2C, and S1](#)), and by darker, single axial structures corresponding to the bases of these parapodia ([Figures 1B, 1C, 2A–2D, 3, and S1](#)). Three-dimensional patches of variable sizes and shape along various sections of the gut, and well beyond the mouth, suggest active mud infill ([Figures 1B, 1K, S1D, and S2A](#)).

Parapodia are identical in morphology on all segments (e.g., [Figures 1D–1F](#)) and are large relative to the body width, up to half the width of the chaetiger to which they are attached. All chaetae are of the simple capillary type, and notochaetae and neurochaetae are of similar morphology and length. They are extremely fine in comparison with other Burgess Shale polychaetes, at approximately 10–28  $\mu\text{m}$  wide (e.g., [Figures 2I–2N](#)). The longest chaetae relative to body size are about two to four times as long as the width of associated chaetigers ([Figures 2I–2N](#)). A maximum of 16 neurochaetae radiate as a tightly clustered fan at an angle roughly perpendicular to the anteroposterior axis of the animal ([Figures 2I–2N](#)). A maximum of 12 notochaetae project posteriorly and tend to be slightly more fanned out ([Figures 2I and 2L](#)). The pygidium is indistinct, and there is no evidence of pygidial cirri.

## Ecology

The presence of a median antenna and the elongate sensory palps both suggest an active lifestyle. Although *K. barbarensis*

has long chaetae, they do not appear to have any specializations for swimming, as has been suggested for the Cambrian taxon *Canadia spinosa* [14]. Like the majority of Cambrian forms (except for *C. spinosa* and potential infaunal forms such as *Peronochaeta dubia* [14]), *K. barbarensis* was most likely an epibenthic deposit feeder (supported by gut infills) that used its notochaetae for defense [15, 16]. The uniramous parapodia on the peristomium and their positioning lateral to the mouth may have speculatively supported buccal musculature useful for expanding the mouth to engulf food particles.

## Phylogenetic Analysis

We performed a phylogenetic analysis using a revised matrix from [3] (see [STAR Methods](#) for a description of character coding changes and the parameters of our phylogenetic analyses). *K. barbarensis* and the Cambrian taxa *Burgessochaeta setigera*, *Phragmochaeta canicularis*, and *C. spinosa* fall into a stem-group position to the crown group as in previous analyses [16, 17], although in a polytomy ([Figure 4A](#)). A complementary parsimony analysis is less well resolved, retrieving the same taxa in a polytomy with other members of the crown group ([Figure S4](#)). These results suggest that Cambrian forms, which are anatomically simpler than most modern forms in terms of body regionalization and specialization of chaetae, share a number of morphological similarities. This simple body morphology is predicted by ancestral state reconstructions based on phylogenomic and transcriptomic datasets [1, 2], but there is less confidence regarding the head and its attendant structures [4]. Structures such as the nuchal organs and eyes are expected in the ancestral annelid but are not found in the Cambrian fossil record, although this lack of evidence may be taphonomic due to their generally small size and presumably low preservation potential. Although a median antenna is generally considered to be a derived character in annelids, it is present in both errant and sedentary clades (i.e., Phyllodocida, Eunicida, Amphinomida, Paraonidae, and some Spionida [7]), where it follows similar innervation patterns [10]. Although possibly homologous, *K. barbarensis* is the only Cambrian polychaete with this structure, suggesting an autapomorphy.

## The “Metameric Head Hypothesis”

Parry et al. [16] recently proposed a “metameric hypothesis” for the origin of the annelid head, based on their reinterpretations of several Cambrian polychaetes (see also [3]). In their framework, the ancestral annelid would have appeared very similar to *P. canicularis*, that is, a uniformly bristled epibenthic worm with an anterior segment with biramous chaetae-bearing parapodia

(B and C) Paratype (ROMIP64389): anterior section showing well-preserved internal head features and sediment infill within the gut (B); elemental map showing phosphatized areas, interpreted as possible remnants of vascularized tissues, within the palps, head, and basal portion of parapodia (C). A thin carbon line running from the front of the head to the palps represents putative neural tissues (see close-up in [Figures 2A and 2B](#)).

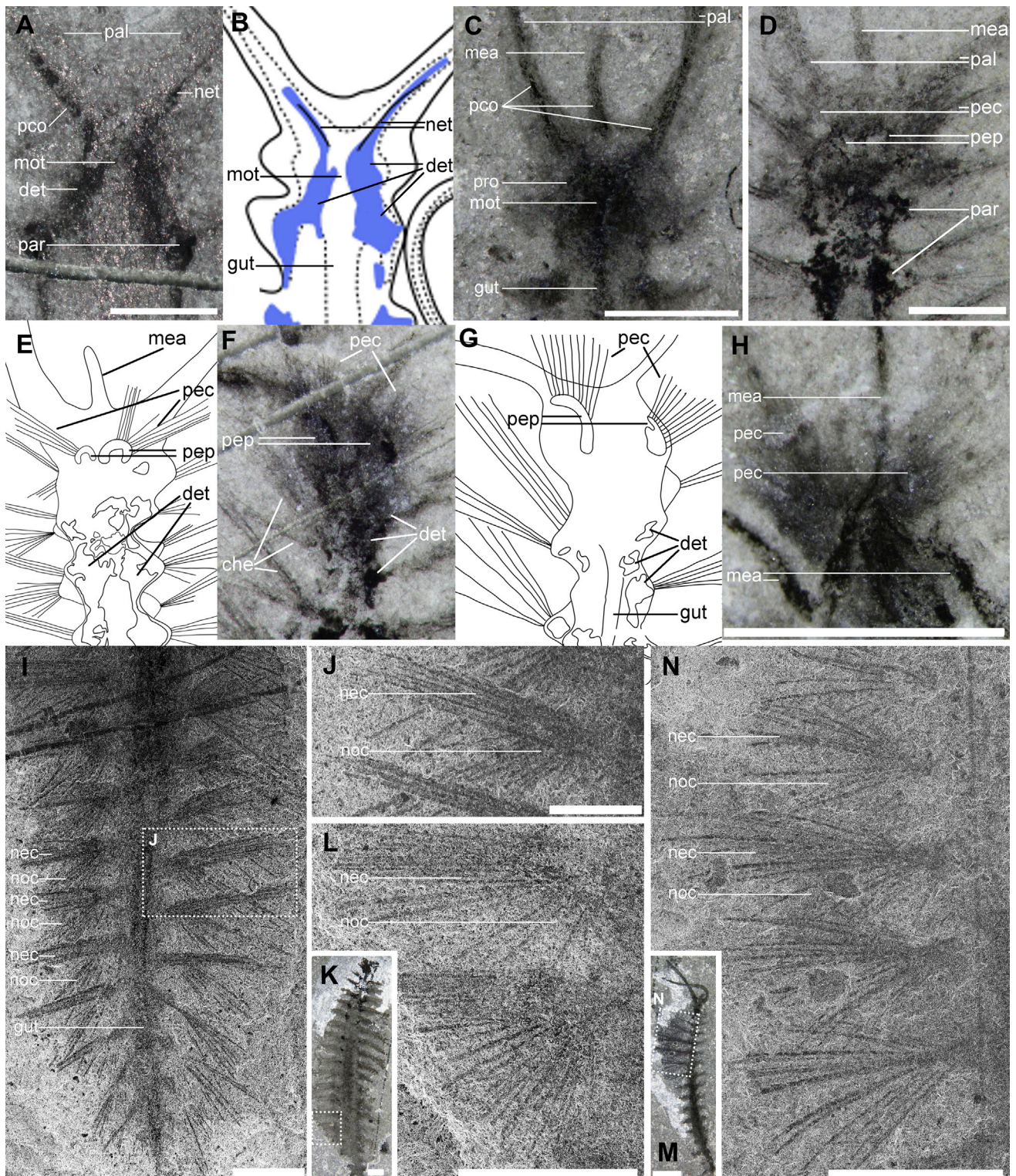
(D and E) Paratype (ROMIP64390): paratype alongside putative *K. barbarensis* juvenile specimens (D); detail showing parapodia preserved in darker black (E).

(F and G) Paratype (ROMIP62972): specimen showing varying parapodial angles and proximal portions of chaetae (F); close-up anterior section (G).

(H) Two paratypes (ROMIP64391.1 [left] and ROMIP64391.2 [right]): two complete specimens with elongate chaetae, median antenna, and palps.

(I and J) Picture showing seven *K. barbarensis* specimens, including one paratype (ROMIP63099.1—see star on figured specimen) (I); close-up showing a putative juvenile of *K. barbarensis* preserved with long chaetae (J).

(K–N) Paratype (ROMIP64392.1-right): overall view of paratype with palps, median antenna, and mud-filled gut extending through the entire body (paratype partially overlaying a second specimen to the left) (K); close-up of anterior gut section (L); close-up of posterior gut section (M); close-up of the left palp showing distal flattening (N).



**Figure 2. Head, Parapodial, and Chaetal Morphology of *Kootenayscolex barbarensis* from the Burgess Shale, Marble Canyon Locality**

(A–C) Specimens showing putative location of mouth and internal tissues within palps and median antenna (C).

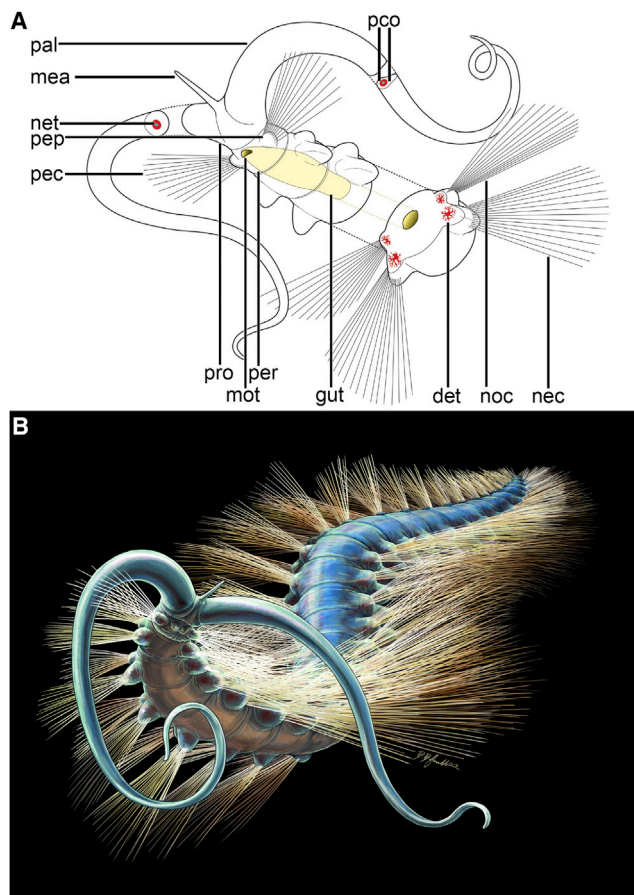
(A and B) Close-ups of boxed area in Figure 1B using direct light (A) and a composite line drawing of Figure 1B and Figure 1C (B).

(C) Paratype (ROMIP64393): superimposed images of both part and counterpart using Apply Image and overlay blending mode in Adobe Photoshop CS6.

(D–H) Specimens showing palps, median antenna (except G), and peristomial chaetae directed anteriolaterally

(D) Close-up of boxed area in Figure 1A.

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**Figure 3. Anatomy of *Kootenayscolex barbarendis* from the Burgess Shale**

(A) Oblique view of the head. Dashed lines indicate cut-away transverse cross sections. Red: vascular tissue; blue: putative neural tissue; yellow: mouth and gut. per, peristomium. For other acronyms, see Figure 1.

(B) Life reconstruction. Image © Royal Ontario Museum, Danielle Dufault. See also Figures S1–S3.

in lieu of a true prostomium. *C. spinosa* was suggested to represent a transitional form where the prostomial notopodia had developed into sensory palps while retaining prostomial neurochaetae.

The metameric head hypothesis is problematic for several reasons. One, it would imply that the last common ancestor of annelids and its closest sister group might bear a body completely

covered in chaetae or sclerites, a position potentially occupied by wiwaxiids [18]. However, the presence of an unambiguous molluscan radula in wiwaxiids [19] makes this scenario rather conjectural. The phylum-level inter-relationships of the lophotrochozoans are also far from resolved, with molecular datasets routinely recovering either Nemertea or Brachiopoda as closer to Annelida than Mollusca [20, 21], further calling into question the utility of the morphology of wiwaxiids for commenting on the anatomy of the ancestral annelid. Although the most recent total evidence analysis recovers *Wiwaxia corrugata*, *Kimberella quadrata*, and *Odontogriphus omalus* as basal stem-group mollusks [17], the significant morphological gap between these three taxa and the Cambrian polychaetes (with unambiguous parapodia-bearing chaeta) is also difficult to reconcile with an entirely chaetigerous ur-annelid (see also [13]).

The metameric head hypothesis [16] is also problematic in that the prostomium is unequivocally considered pre-segmental. In crown-group Annelida, the prostomium is derived from the region of the annelid embryo corresponding to the prototroch and above, while the segmental body is derived from the growth zone below the metatroch; this embryological division is among the most highly conserved patterns in annelid ontogeny [9, 17]. The metameric head hypothesis would require the *de novo* transformation of a segmental unit into a prostomial unit, and prostomial notopodia into sensory palps. Although it is possible that such transitions occurred within the annelid stem lineage, the metameric head hypothesis does not posit any plausible mechanism for this alteration to the fundamental ground pattern of the crown-group Annelida.

Considering *P. canicularis* to be close to an ancestral form, a central pillar of the metameric head hypothesis, is also problematic on taphonomic grounds, as this taxon is rare and poorly preserved [22]. Similar “head” morphologies, with bundles of chaetae pointing anteriorly, are found in many Burgess Shale polychaetes, including in *B. setigera* [21, 23], because the head is usually buried at an angle relative to the rest of the body in most specimens (Figure S3K).

Furthermore, when the metameric head hypothesis was developed, it relied on *C. spinosa* bearing a transitional prostomial morphology to illustrate the plausibility of a prostomium simultaneously bearing palps and notopodia+chaetae. Although a complete redescription of *C. spinosa* is beyond the scope of this paper, we interpret the prostomium with ventral parapodia [5] as a parapodia-bearing segment directly posterior to a small prostomium (i.e., on the peristomium), since there is no evidence that the head is buried at an angle or deformed (Figures S3G and S3H). A similar configuration is also seen in *B. setigera* (Figures

(E) Line drawing of (D).

(F) Paratype (ROMIP64394).

(G) Line drawing of (F).

(H) Paratype (ROMIP64395).

(I) Close-up of boxed area in Figure 1H.

(J) Close-up of chaetal bundle.

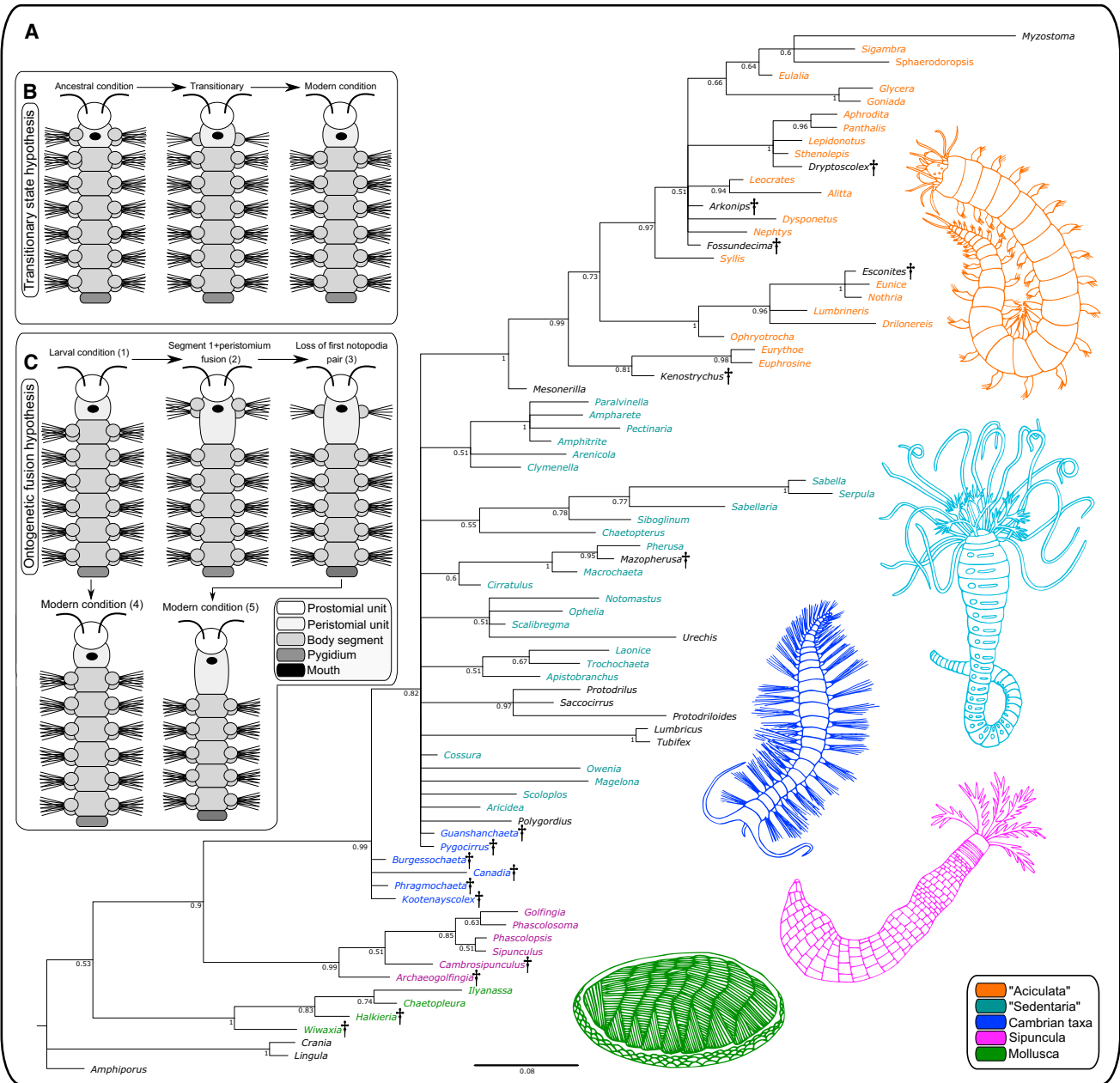
(K) ROMIP64396.

(L) Close-up of chaetal bundle.

(M) ROMIP64397.

(N) Close-up of chaetal bundle.

(A)–(H), (K), and (M) are cross-polarized light images; (I), (J), (L), and (N) are scanning electron microscope images. For acronyms, see Figure 1. Scale bars, 1 mm. See also Figures S1–S3.



**Figure 4. Evolutionary Implications of *Kootenayscolex barbarensis***

(A) Phylogenetic position of *K. barbarensis* using majority-rule Bayesian analysis (parameters are detailed in STAR Methods). Numbers at nodes are posterior probabilities. Orange: taxa historically considered part of the major clade “Aciculata”; blue: taxa historically considered part of the ecomorphotype “Sedentaria”; dark blue: Cambrian taxa; pink: sipunculids; green: mollusks.

(B and C) Two scenarios for annelid head evolution that invoke modern developmental plasticity.

(B) Modern polychaete head arising from a hypothesized ancestor with a biramous peristomium losing the notopodia and notochaetae to produce a uniramous Cambrian condition, then losing the first neuropodia and neurochaeta, leading to the crown-group Annelida.

(C) Alternatively, the uniramous peristomium of *K. barbarensis* and *C. spinosa* may have been produced during ontogeny (see text for descriptions of each numbered step).

See also Figure S4.

S3I and S3J). Like *C. spinosa* and *K. barbarensis*, the fact that this segment bears both the mouth and parapodia (presumably uniramous) + chaetae leads us to conclude that it is homologous with the peristomium of extant annelids.

**The “Chaetigerous Mouth Hypothesis”**

*K. barbarensis*, *C. spinosa*, and *B. setigera* fall into a stem polytomy (Figure 4A) suggesting that their unique peristomial morphology is plesiomorphic and does not represent an

autopomorphy of these Cambrian polychaetes. This leads us to propose a new hypothesis for the development of the modern annelid head. This is particularly true with regards to the location of the mouth, which up to this point has remained unclear in Cambrian annelids [16].

Rather than a metameric origin for the entire annelid head, whereby an anteriormost chaetigerous unit transitions into both prostomium and peristomium in the crown group (within which both are apodous+achaetigerous), we propose a segmental or chaetigerous origin for only the peristomial portion of the annelid head. Although further fossil evidence is required to corroborate this view, our hypothesis suggests a total-group annelid ancestor that is less of a radical departure from the ground pattern of the crown-group Annelida compared to Parry et al. [3].

Using this framework, the ancestral annelid would have had a small prostomium with two palps (as is generally predicted [1, 2, 4]) and a segmented body, bearing a mouth as well as biramous parapodia+chaetae on the peristomium (although there are as yet no unequivocal fossils showing this biramous condition; Figures 4B and 4C). The uniramous peristomium found in *K. barbarensis*, *B. setigera*, and *C. spinosa*, as well as the modern condition of an apodous peristomium, could have come about through one of two related developmental pathways.

The parapodia and chaetae of the ancestral mouth-bearing segment may have been lost in a manner similar to that which occurs during the development of at least three species within the genus *Magelona*, which possess “transient parapodia” and “transient chaetae” [24]. These transient structures occur on segments 1 and 2 during the larval stage but are subsequently lost after metamorphosis. The Cambrian uniramous peristomium condition may represent a “transitional state” whereby the notopodia were lost in the ancestrally biramous mouth-bearing segment through a developmental mechanism similar to that in the magelonids (“transitional” stage in Figure 4B). The neuropodia and neurochaetae of this transitional peristomium would be lost before the advent of the crown-group annelids, leading to the modern apodous and achaetigerous head.

Alternatively, Cambrian polychaetes may evidence a developmental process unique to the Cambrian, but which may also have parallels in the developmental biology of extant polychaetes, such as the nereidids. In the nereidid *Hediste diversicolor* [25] (also the genera *Laeonereis* [26] and *Platynereis* [27]), the adult peristomium is developed through the fusion of the first larval chaetiger, which bears parapodia and chaetae, to the larval peristomium. The parapodia of the first larval chaetiger are re-absorbed or “aborted” during fusion, after which they form the posterior tentacular cirri. The uniramous mouth segment of *K. barbarensis* may have been derived from a similar process (Figure 4C), whereby (1) the larvae of the Cambrian taxa may have appeared morphologically modern with an apodous mouth-bearing segment, (2) the first body segment fused with the mouth segment during ontogeny, and (3) the notopodia and notochaetae were lost prior to adulthood using a developmental mechanism similar to the one seen in the nereidids to produce the morphology seen in *K. barbarensis*, *B. setigera*, and *C. spinosa*. In this context, the modern polychaete head morphology was derived from a larva with an apodous peristomium (4), or a fused mouth and body segment may have subse-

quently lost the neuropodia and chaetae to give rise to the extant peristomial apodous+achaetigerous condition (5).

An elevated degree of plasticity in gene regulatory networks during the dawn of the metazoans has been invoked as a contributor to the rapid appearance of nearly all major phyla during the Cambrian Explosion [27–29]. Therefore, while direct evidence of developmental biology is difficult to document from early Palaeozoic fossils—although some data are available in fossilized embryos [30, 31]—it should be expected that continued observations of early fossil taxa will yield morphologies that would have been difficult, if not impossible, to anticipate based solely on extant lineages. In this way, *K. barbarensis* joins similar discoveries of early arthropods [32], mollusks [17], and hemichordates [33] that complement ontogenetic studies to unveil the origins of body plans before developmental canalization concomitant with the establishment of modern phyla [34].

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND SOFTWARE AVAILABILITY

## SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures, one table, and one dataset and can be found with this article online at <https://doi.org/10.1016/j.cub.2017.12.019>.

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## AUTHOR CONTRIBUTIONS

Both authors conceived the project, made observations, analyzed the data, created figures, and wrote the manuscript. K.N. took morphometric measurements. J.-B.C. led fieldwork activities and prepared and photographed the material.

## DECLARATION OF INTERESTS

The authors declare no competing interests.



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## REFERENCES

- Struck, T.H., Paul, C., Hill, N., Hartmann, S., Hösel, C., Kube, M., Lieb, B., Meyer, A., Tiedemann, R., Purschke, G., and Bleidorn, C. (2011). Phylogenomic analyses unravel annelid evolution. *Nature* **471**, 95–98.
- Weigert, A., Helm, C., Meyer, M., Nickel, B., Arendt, D., Hausdorf, B., Santos, S.R., Halanych, K.M., Purschke, G., Bleidorn, C., and Struck, T.H. (2014). Illuminating the base of the annelid tree using transcriptomics. *Mol. Biol. Evol.* **31**, 1391–1401.
- Parry, L.A., Edgecombe, G.D., Eibye-Jacobsen, D., and Vinther, J. (2016). The impact of fossil data on annelid phylogeny inferred from discrete morphological characters. *Proc. Biol. Sci.* **283**, 20161378.
- Eibye-Jacobsen, D., and Vinther, J. (2012). Reconstructing the ancestral annelid. *J. Zool. Syst. Evol. Res.* **50**, 85–87.
- Caron, J.-B., Gaines, R.R., Aria, C., Mángano, M.G., and Streng, M. (2014). A new phyllopod bed-like assemblage from the Burgess Shale of the Canadian Rockies. *Nat. Commun.* **5**, 3210.
- Caron, J.-B., and Jackson, D.A. (2006). Taphonomy of the Greater Phyllopod Bed Community, Burgess Shale. *Palaios* **21**, 451–465.
- Rouse, G.W., and Pleijel, F. (2001). *Polychaetes* (Oxford: Oxford University Press).
- Wilson, P., Parry, L.A., Vinther, J., and Edgecombe, G.D. (2016). Unveiling biases in soft-tissue phosphatization: extensive preservation of musculature in the Cretaceous (Cenomanian) polychaete *Rollinschaeta myoplana* (Annelida: Amphinomididae). *Palaeontology* **59**, 463–479.
- Heuer, C.M., and Loesel, R. (2008). Immunofluorescence analysis of the internal brain anatomy of *Nereis diversicolor* (Polychaeta, Annelida). *Cell Tissue Res.* **331**, 713–724.
- Orrhage, L., and Müller, M.C.M. (2005). Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* **535/536**, 79–111.
- Zanol, J. (2010). Homology of prostomial and pharyngeal structures in eunicida (Annelida) based on innervation and morphological similarities. *J. Morphol.* **271**, 1023–1043.
- Heuer, C.M., Müller, C.H., Todt, C., and Loesel, R. (2010). Comparative neuroanatomy suggests repeated reduction of neuroarchitectural complexity in Annelida. *Front. Zool.* **7**, 13.
- Eibye-Jacobsen, D. (2004). A reevaluation of *Wiwaxia* and the polychaetes of the Burgess Shale. *Lethaia* **37**, 317–335.
- Conway Morris, S. (1979). Middle Cambrian polychaetes from the Burgess Shale of British Columbia. *Philos. Trans. R. Soc. B Biol. Sci.* **285**, 227–274.
- Westheide, W. (1997). The direction of evolution within the Polychaeta. *J. Nat. Hist.* **31**, 1–15.
- Parry, L., Vinther, J., and Edgecombe, G.D. (2015). Cambrian stem-group annelids and a metameric origin of the annelid head. *Biol. Lett.* **11**, 1–5.
- Vinther, J., Parry, L., Briggs, D.E.G., and Van Roy, P. (2017). Ancestral morphology of crown-group molluscs revealed by a new Ordovician stem aculiferan. *Nature* **542**, 471–474.
- Zhang, Z., Smith, M.R., and Shu, D. (2015). New reconstruction of the *Wiwaxia* scleritome, with data from Chengjiang juveniles. *Sci. Rep.* **5**, 14810.
- Smith, M.R. (2012). Mouthparts of the Burgess Shale fossils *Odontogriphus* and *Wiwaxia*: implications for the ancestral molluscan radula. *Proc. Biol. Sci.* **279**, 4287–4295.
- Dunn, C.W., Hejnal, A., Matus, D.Q., Pang, K., Browne, W.E., Smith, S.A., Seaver, E., Rouse, G.W., Obst, M., Edgecombe, G.D., et al. (2008). Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* **452**, 745–749.
- Kocot, K.M., Struck, T.H., Merkel, J., Waits, D.S., Todt, C., Brannock, P.M., Weese, D.A., Cannon, J.T., Moroz, L.L., Lieb, B., and Halanych, K.M. (2017). Phylogenomics of lophotrochozoa with consideration of systematic error. *Syst. Biol.* **66**, 256–282.
- Conway Morris, S., and Peel, J.S. (2008). The earliest annelids: lower Cambrian polychaetes from the Sirius Passet Lagerstätte, Peary Land, North Greenland. *Acta Palaeontol. Pol.* **53**, 137–148.
- Schroeder, P.C., and Hermans, C.O. (1975). *Annelida: Polychaeta. In Reproduction of Reproduction of Marine Invertebrates III: Annelids and Echiurans*, A.C. Giese, and J.S. Pearse, eds. (New York: Academic Press).
- Wilson, D.P. (1982). The larval development of three species of *Magelona* (Polychaeta) from localities near Plymouth. *J. Mar. Biol. Assoc. UK* **62**, 385–401.
- Dales, R.P. (1950). The reproduction and larval development of *Nereis diversicolor* O.F. Müller. *J. Mar. Biol. Assoc. UK* **29**, 321–360.
- Mazurkiewicz, M. (1975). Larval development and habits of *Laeonereis culveri* (Webster) (Polychaeta: Nereidae). *Biol. Bull.* **149**, 186–204.
- Fischer, A.H., Henrich, T., and Arendt, D. (2010). The normal development of *Platynereis dumerilii* (Nereididae, Annelida). *Front. Zool.* **7**, 31.
- Davidson, E.H., and Erwin, D.H. (2006). Gene regulatory networks and the evolution of animal body plans. *Science* **311**, 796–800.
- Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., and Peterson, K.J. (2011). The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* **334**, 1091–1097.
- Maas, A., Braun, A., Dong, X.P., Donoghue, P.C.J., Müller, K.J., Olempska, E., Repetski, J.E., Siveter, D.J., Stein, M., and Waloszek, D. (2006). The “Orsten”—More than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. *Palaeoworld* **15**, 266–282.
- Yin, L., Zhu, M., Knoll, A.H., Yuan, X., Zhang, J., and Hu, J. (2007). Doushantuo embryos preserved inside diapause egg cysts. *Nature* **446**, 661–663.
- Aria, C., and Caron, J.-B. (2017). Burgess Shale fossils illustrate the origin of the mandibulate body plan. *Nature* **545**, 89–92.
- Nanglu, K., Caron, J.-B., Conway Morris, S., and Cameron, C.B. (2016). Cambrian suspension-feeding tubicolous hemichordates. *BMC Biol.* **14**, 56.
- Peterson, K.J., Dietrich, M.R., and McPeck, M.A. (2009). MicroRNAs and metazoan macroevolution: insights into canalization, complexity, and the Cambrian explosion. *BioEssays* **31**, 736–747.
- Caron, J.-B., and Jackson, D.A. (2008). Paleoeology of the Greater Phyllopod Bed community, Burgess Shale. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **258**, 222–256.

## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
Fossil polychaete <i>Kootenyscolex barborensis</i>	Royal Ontario Museum	See <a href="#">Table S1</a> for details
Software and Algorithms		
Adobe Photoshop	Adobe Systems	CS6
ImageJ	National Institutes of Health, Public domain	1.46r
TEAM software for silicon drift detector on FEI Quanta 200 FEG scanning electron microscope	EDAX, Materials Analysis Division of AMETEK	4.1
TNT	Willi Hennig Society	1.5
MrBayes	Huelsenbeck, Larget, van der Mark, Ronquist, Simon, and Teslenko	3.2.6

### CONTACT FOR REAGENT AND RESOURCE SHARING

Requests for further information should be directed to and will be fulfilled by the Lead Contact, Karma Nanglu ([karma.nanglu@mail.utoronto.ca](mailto:karma.nanglu@mail.utoronto.ca)).

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

The material comes from two localities within the middle Cambrian (Stage 5) Burgess Shale. 515 come from specimens from Marble Canyon Quarry in Kootenay National Park, previously referred as “*Burgessochaeta cf. setigera*” in [5]. 8 specimens, including ROMIP57190.1-2 and ROMIP64399 (Figures S3A–S3F) come from Walcott Quarry, Yoho National Park (previously referred to as in-det “polychaeta D” [35]). All specimens are from the “thick” Stephen Shale Formation. See [Table S1](#) for further details.

### METHOD DETAILS

Some specimens were mechanically prepared using a micro-engraving tool equipped with a carbide bit to reveal features buried in the matrix. Specimens were observed using a stereo microscope and photographed using direct or cross-polarized light on dry or wet specimens. Images of the part and counterpart of some specimens were blended together using Apply Image and overlay blending mode in Adobe Photoshop CS6 to summarize information preserved on both sides. Measurements of morphology were made using the program ImageJ 1.46r. Secondary electron micrographs, backscatter scanning electron images and elemental maps were obtained using an environmental scanning electron microscope (FEI Quanta 200 FEG) equipped with an energy scanning spectroscopy (EDS) X-ray detector and octane plus silicon drift detector (SDD, using TEAM software, Version 4.1) under low vacuum conditions (70 Pa, 15 Kv, 400  $\mu$ s dwell time) at the University of Windsor Great Lakes Institute for Environmental Research, Canada.

### QUANTIFICATION AND STATISTICAL ANALYSIS

The Bayesian phylogenetic analysis was conducted using MrBayes 3.2.6 using the same search parameters as [3]: 10 million generations, sampling every 1,000 generations, 25% burn-in, using an mkv model with a gamma distribution for rate variation. The parsimony analysis was conducted using TNT 1.5 following [3]: 1,000 initial addition sequences, 10,000 replicates for calculating Jackknife frequencies, instructed to find optimal topology 10 times. Changes to the matrix from [3] were as follows: (1) all prostomial and pygidial characters for *Phragmochaeta* (Figure S1A in [3]) were recoded as unknown to accommodate its incompleteness; (2) character 115 was modified into “*Prostomium+achaetigerous peristomium*”: 0 - absent –; 1- present. *Kootenayscolex*, *Canadia*, and *Burgessochaeta* were coded as 0, all extant polychaetes were coded as 1; (3) characters 116 and 117 were deleted as they are equivocal based on our re-interpretations of Cambrian annelid morphology.

### DATA AND SOFTWARE AVAILABILITY

The character matrix used in our phylogenetic analyses is available for download as [Data S1](#). This published work and the nomenclatural acts it contains have been registered in ZooBank: <http://zoobank.org/References/2EE9BD6E-E6BC-4BC8-995D-08B1CC858B12>